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Morphology and Taxonomy of the Japanese *Rhodymeniales* (1) Thallus Structure and Reproductive Organs of *Lomentaria lubrica* (*Lomentariaceae*, *Rhodophyta*)

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Detailed morphological studies have been carried out on the vegetative thallus and reproductive organs of *Lomentaria lubrica* collected from Sai, Aomori Prefecture, Japan. This is the first report of male gametophytes and carposporophyte formation in the species. The thallus structure is multiaxial, hollow, and is composed of a one-layered cortex and a one or two-layered medulla surrounding the central cavity. The transverse septum occurs only at the base of the branch or branchlet. The cortical cells cut off small cells around them. The medullary cells longitudinally border the cortical cells and solely bear secretory cells. The procarp is composed of a three-celled carpogonial branch and a two-celled auxiliary cell branch. After fertilization, the cells of the carpogonial branch are fused. The fused carpogonial branch directly touches the auxiliary cell. The primary gonimoblast is cut off transversely from the auxiliary cell. Gonimoblasts develop outwards from large fusion cells. Most gonimoblasts transform into carposporangia. The carposporophyte is covered with pericarp. The mature cystocarp is urceolate and has an ostiole. Spermatangia are cut off from mother cells produced on the cortical cells. Tetrasporangia are terminally produced on the cortical cells, tetrahedrally divided, and formed in the depressed sori.

Key words: Carposporophyte formation, *Lomentaria lubrica*, morphology, *Rhodophyta*, *Rhodymeniales*.

Lomentaria lubrica (Yendo) Yamada, an endemic species distributed in northern Honshu, Japan, was first described by Yendo (1920) as *Chylocladia lubrica* from Oma, Aomori Prefecture. Yamada (1932) later transferred it from *Chylocladia* to *Lomentaria* on noting the absence of a diaphragm (transverse septum) and tetrasporangia protruding into the cavity. Kawashima (1960) observed the thallus structure and tetrasporangia formation. The male gametophytes and carposporophyte formations are still unknown. Recently, we collected *L. lubrica* including male and female gametophytes and tetrasporophytes from Sai, also in Aomori Prefecture, and describe here the detailed morphological features. The findings allow further examination of the taxonomic position of *L. lubrica*.

Materials and Methods

Used specimens were collected at Sai, Shimokita Co., Aomori Prefecture (41°27'N, 141°52'E) on 4 August 2005 (Fig. 1). Specimens were preserved in 10% formalin/seawater. Voucher herbarium specimens are deposited at TNS. The specimens were sectioned by a freezing microtome, and sections

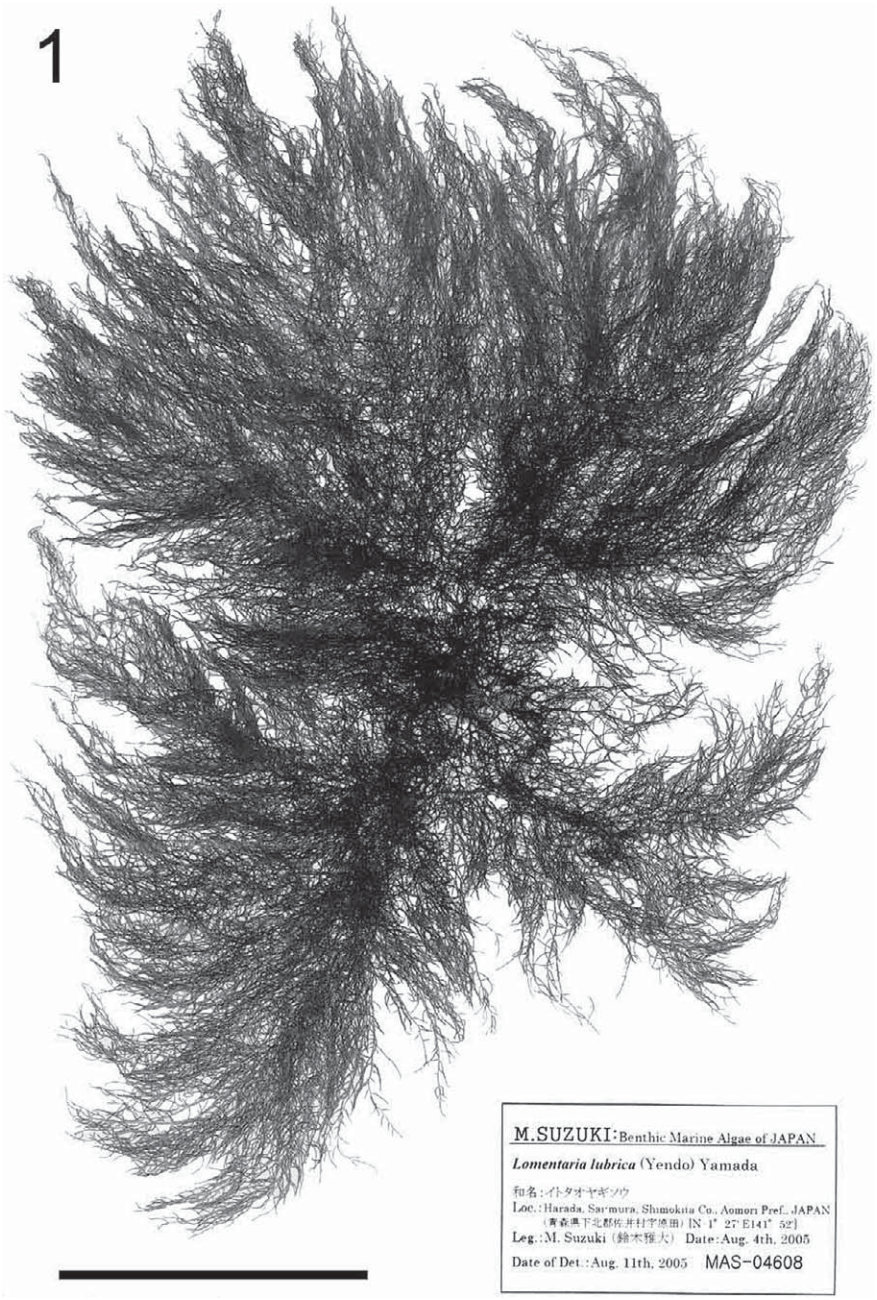


Fig. 1. Voucher specimen of *Lomentaria lubrica*. (TNS-AL-161634, August 4, 2005, Sai, Shimokita Co., Aomori Pref.). Scale = 10 cm.

were stained with 1% erythrosin or 0.5% cotton blue, and mounted in 50% Karo syrup. Drawings were made with a camera lucida.

Results

Lomentaria lubrica (Yendo) Yamada in J. Fac. Sci., Hokkaido Imper. Univ., Ser. V (Bot.) **1** (3): 121 (1932).

Japanese name: Ito-taoyagisô.

Type locality: Oma, Shimokita Co., Aomori Prefecture, Japan.

Distribution: Mutsu Bay (Yamada 1928); Tsugaru Strait (Takamatsu 1938); Sai, Aomori Prefecture (Kawashima 1960).

Specimen examined: Sai (41°27'N, 141°52'E), Shimokita Co., Aomori Prefecture, Japan. (4 August

Fig. 2–3. Habit of *Lomentaria lubrica*. Fig. 2. Cystocarpic plant bearing cystocarps (arrows). Fig. 3. Tetrasporangial plant bearing tetrasporangial sori (arrows). Scale = 5 mm.

2005, M. Suzuki, cystocarpic TNS-AL-161633, spermatangial TNS-AL-161635, tetrasporangial TNS-AL-161634).

External morphology (Figs. 1–3)

The plants grow on rocks or on the thallus of *Sargassum* spp. or *Laurencia* spp. attached by small discoid holdfast, 0.5 to 1 mm in diameter. Usually, two or three plants grow caespitose, forming tufts. The thallus is erect, flaccid, filiform, mucilaginous, light to pale red or greenish red, to 20 cm in height, much branched dichotomously, with or without percurrent axes. The short branchlets alternately or oppositely produced at the upper parts giving an irregularly branching appearance. The branches are cylindrical, slender, unconstricted, 1.0 to 1.5 mm in diameter. The branchlets terete, rarely constricted at the base, 2.0 to 6.0 mm in length, 0.2 to 0.5 mm in diameter. The specimen firmly adhered to paper on drying.

Thallus structure (Figs. 4–7)

Thallus structure multiaxial with a cluster of apical cells (Fig. 4), hollow, composed of one-layered cortex and one or two-layered medulla surrounding the central cavity (Figs. 5, 6). The transverse septum occurs only at the base of the branch or branchlet. At the upper parts of the branches or branchlets, the cortical cells are rectangular or polygonal,

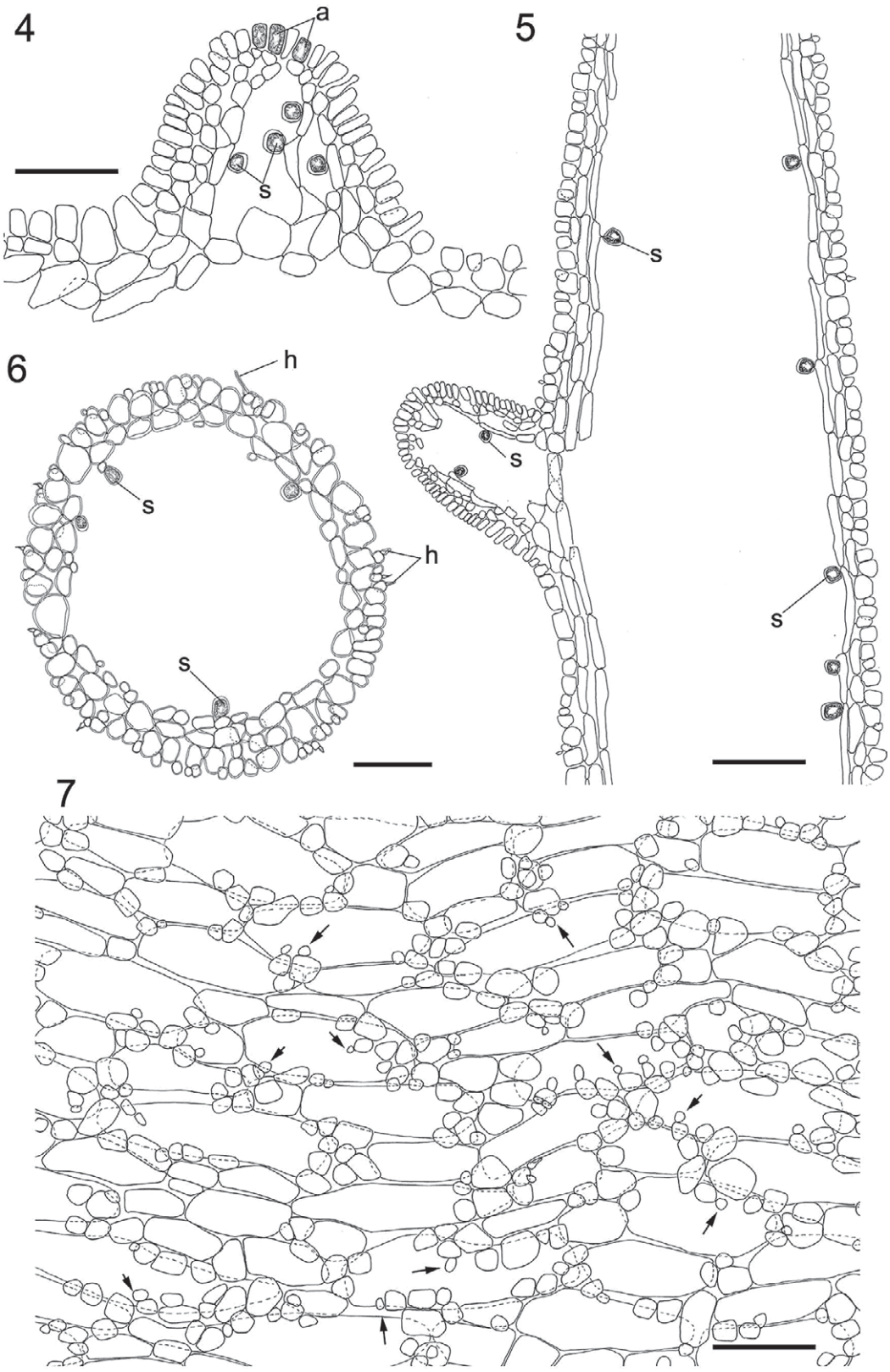


Fig. 4–7. Thallus structure of *Lomentaria lubrica*. Fig. 4. Longitudinal section of apical part of thallus. Fig. 5. Longitudinal section of middle part of thallus. Fig. 6. Transverse section of middle part of thallus. Fig. 7. Surface view of middle part of thallus. The small cells (arrows) around cortical cells forming rosettes like appearance. Scale = 50 μm. a: Apical cell. h: Hair cell. s: Secretory cell.

uniform and regularly arranged, 5.5 to 10 μm in length, 2.5 to 6.0 μm in width, 10 to 20 μm in thickness, whereas at the middle to lower parts of the branches, they are round to polygonal, irregularly arranged, 15 to 33 μm in length, 10 to 28 μm in width, 15 to 27 μm in thickness, and cut off the small cells around them. The small cells are round, 5.0 to 11 μm in diameter, and often cut off a unicellular hair (Fig. 6). In surface view, the cortical cells are irregularly and loosely arranged, underlying the medullary cells were visible through the cortex; the small cells around cortical cells form rosette-like appearance (Fig. 7). The medullary cells are elongate rectangular, longitudinally border the cortical cells, 17 to 57 μm in length, 8 to 30 μm in width, 4 to 18 μm in thickness, solely bear secretory cells (gland cells). The secretory cells are round to pyriform, 10 to 13 μm in length, 8 to 11 μm in diameter.

Life history

The gametophytes are dioecious: The tetrasporophyte and gametophyte are uniform. Therefore, the life history is isomorphic
(*Polysiphonia* type).

Female gametophyte (Figs. 2, 8–13)

The cystocarps protrude from the surface of the thallus, sessile, developed solely, scattered on the upper part of branches or branchlets of the female gametophyte (Fig. 2).

The procarp is composed of a three-celled carpogonial branch and a two-celled auxiliary cell branch (Fig. 8). The supporting cell uniform with a small cell cuts off from cortical cell, 10 to 11 μm in length, 7.5 to 13 μm in diameter. The first and second cell of carpogonial branch are cubic, 5.0 to 6.0 μm in length, 4.0 to 7.0 μm in diameter. The carpogonium is conical, 6.0 to 7.5 μm in length, 2.0 to 2.5 μm in diameter at the base, with a trichogyne. The trichogyne filamentous, protruded from the terminal of carpogonia. The auxiliary mother cell is oblong, 9.5 μm in length, 6.0 μm in diameter. The auxiliary cell is hemispherical, 4.0 μm in length, 7.0 μm in diameter.

After fertilization, the supporting cell, auxiliary mother cell and auxiliary cell are enlarged, and the cells of the carpogonial branch are fused. The fused carpogonial branch directly touches the auxiliary cell (Fig. 9). The primary gonimoblast cuts off transversely from the auxiliary cell. After the diploid nucleus migrates into the auxiliary cell, the carpogonial branch is fused with the supporting cell, and forms a column-like fusion cell (Fig. 10). The auxiliary mother cell begins to fuse with the auxiliary cell and some vegetative cells, and form a large trunk-like fusion cell. The column-like fusion cell reduces in its contents, while the trunk-like fusion cell becomes enlarged (Figs. 11, 12).

The gonimoblasts develop outwards from the trunk-like fusion cell, and form a globose carposporophyte (Figs. 11, 12). As the carposporophyte grows, the gonimoblasts are enlarged. Most gonimoblasts transform into carposporangia (Fig. 13). The mature carposporangium is round to polygonal, 46 to 65 μm in length, 38 to 54 μm in diameter.

The carposporophyte is covered with pericarp. After fertilization, the cortical cells around the procarp begin to divide, and elongate outwards. The mature pericarp is composed of an outer layer and an inner layer. The inner layer is composed of one to two cells that are narrow elliptical or rectangular, not form stellate cells (Fig. 13).

The mature cystocarp is urceolate, and has an ostiole, 0.6 to 1.0 mm in length, 0.5 to 0.6 mm in diameter (Fig. 13).

Male gametophyte (Fig. 14)

Spermatangia develop in sori over the surface of upper parts of branches and branchlets of male gametophyte. The cortical cells abcise two to four spermatangial

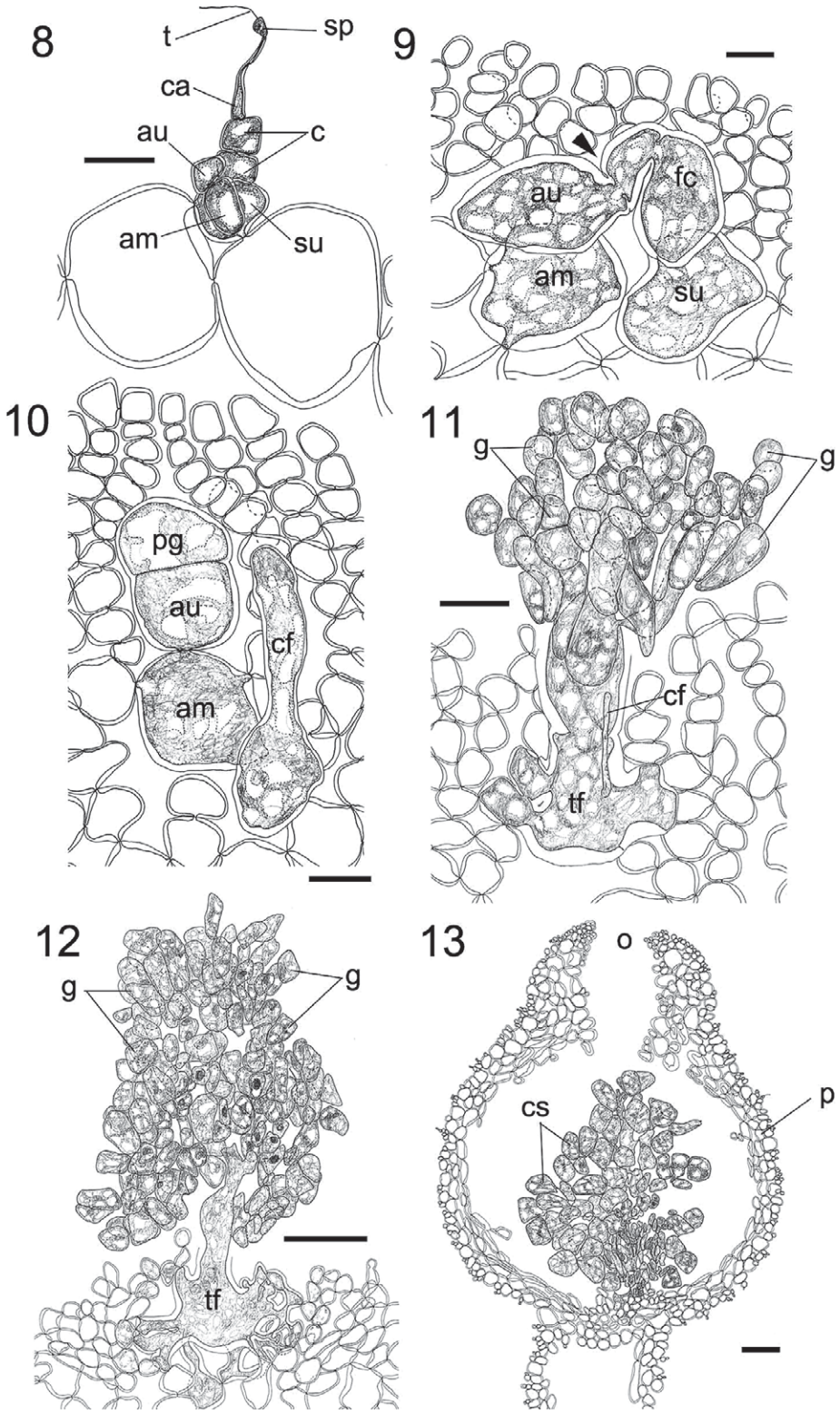
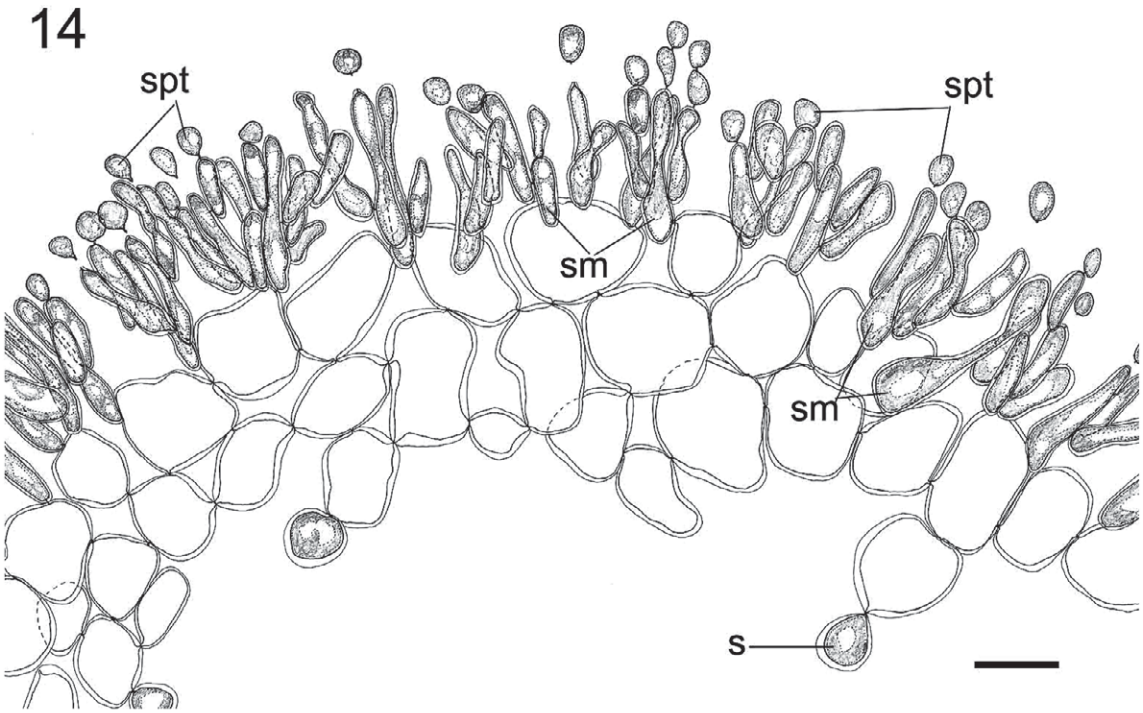


Fig. 8–13. Carposporophyte formation of *Lomentaria lubrica*. Fig. 8. Procarp. Fig. 9. After fertilization. The fused carpogonial branch contacts directly with the auxiliary cell (arrowhead). Fig. 10. Auxiliary cell cut off a primary gonimoblast. Fig. 11, 12. Development of carposporophyte. Fig. 13. Mature cystocarp. Scale = 10 μm (Figs. 8–11); 50 μm (Figs. 12, 13). am: Auxiliary mother cell. au: Auxiliary cell. c: Cells of a carpogonial branch. ca: Carpogonium. cf: Column-like fusion cell. cs: Carposporangium. fc: Fused carpogonial branch. g: Gonimoblast. o: Ostiole. p: Pericarp. pg: Primary gonimoblast. sp: Spermatium. su: Supporting cell. t: Trichogyne. tf: Trunk-like fusion cell.



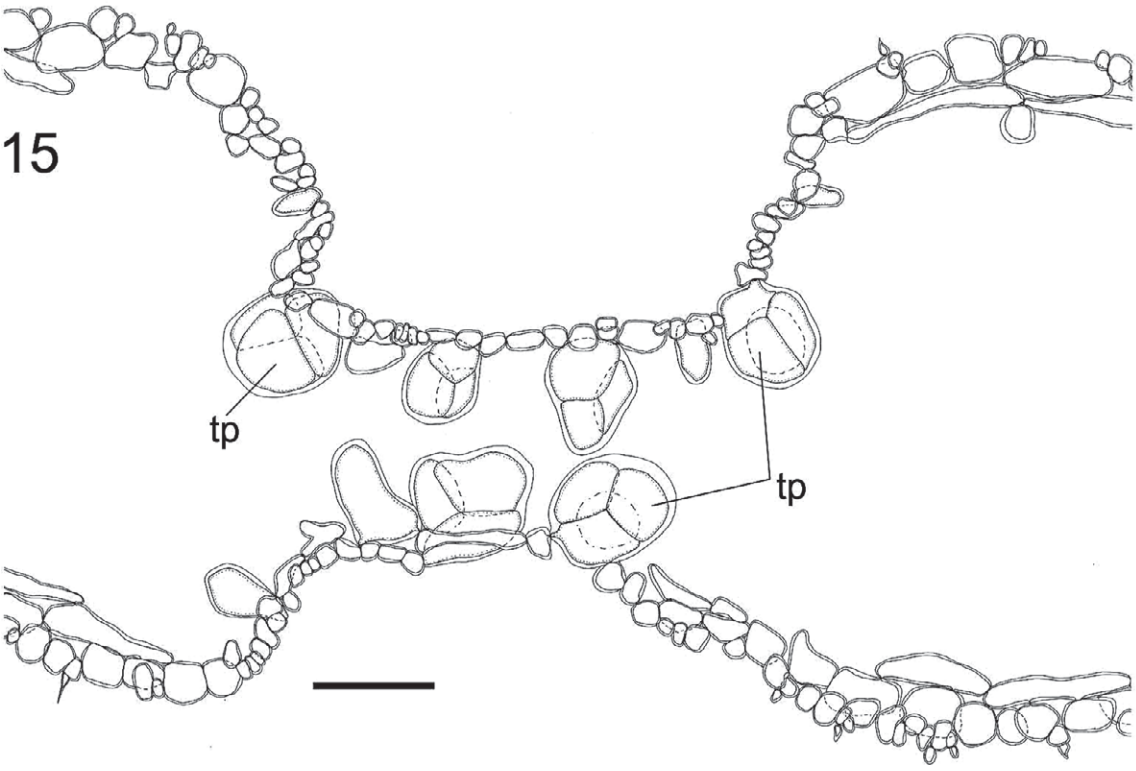


Fig. 14–15. Transverse section of male gametophyte and tetrasporophyte of *Lomentaria lubrica*. Fig. 14. Transverse section of spermatangial sori. Scale = 10 μm. s: Secretory cell. sm: Spermatangial mother cell. spt: Spermatangium. Fig. 15. Transverse section of tetrasporangial sori. Scale = 50 μm. tp: Tetrasporangium.

mother cells around their upper corners. These mother cells cut off laterally one to two secondary mother cells. The spermatangia develop terminally on these mother cells by centripetal constriction. After the liberation of primary spermatangium, the mother cell give rise to secondary spermatangium. These secondary spermatangia are often produced while the primary ones still remain. The primary mother cells rarely have plastids, and are elongate rectangular or lanceolate with a round apex, often slackly constricted at the center, 15 to 24 μm in length, 1.5 to 4.0 μm in diameter. The secondary mother cell is smaller than the primary one, 7.5 to 16 μm in length, 2.0 to 3.5 μm in diameter. The mature spermatangium and spermatium have no plastids, and is elliptical or orbicular, 3.0 to 5.0 μm in length, 3.0 to 4.0 μm in diameter.

Tetrasporophyte (Figs. 3, 15)

Tetrasporangial sori are produced on the upper part of branches and branchlets (Fig. 3). The tetrasporangia are terminally produced on cortical cells, tetrahedrally divided, formed in the depressed sori. The mature tetrasporangium is obovate, 50 to 55 μm in length, 43 to 50 μm in diameter (Fig. 15).

Discussion

The external morphology of *L. lubrica* accords with Yendo (1920), Yamada (1928) and Kawashima (1960). The thallus structure and tetrasporangia formation accord with Kawashima (1960). The terete, irregularly branched and unconstricted thallus is similar to *L. clavellosa* (Irvine and Guiry 1983). The thallus structure is similar to *L. clavellosa* and *L. orcadensis* (Irvine and Guiry 1983) and *L. pinnata* (Suzuki unpublished). They form the transverse septa only at the base of branch and branchlet. *L. lubrica* has small cells cut off from cortical cells. In surface view, these small cells form a rosette-like appearance. The formation of rosettes is similar to *L. australis* (Womersley 1996) and *L. pinnata*. The one-layered cortex and one to two-layered medulla are thinner than the other species. The development of spermatangium of *L. lubrica* accords with *L. hakodatensis* (Tazawa 1975, Lee 1978). The structure of procarp and carposporophyte formation accord with *L. articulata* (Bliding 1928), *L. catenata* and *L. hakodatensis* (Lee 1978), although the structure of the pericarp is thinner than the other species. The formation of tetrasporangium accords with *Lomentaria* species (cf. Bliding 1928, Lee 1978, Irvine and Guiry 1983, Womersley 1996).

The genus *Lomentaria* is characterized by a hollow thallus, three-celled carpogonial branch, mature cystocarp protruding on the thallus, tetrahedrally divided tetrasporangia and tetrasporangia formed in depressed sori (Irvine and Guiry 1983, Womersley 1996 and Yoshida 1998). *Lomentaria lubrica* satisfies the above characteristics. However, *L. articulata* the type species of the genus *Lomentaria* and some other species such as *L. catenata* and *L. hakodatensis* have transverse septa constricting the medullary cavity at regular intervals. Others, such as *L. clavellosa*, *L. orcadensis* and *L. pinnata* have septa occurring only at the base of branches and branchlets, where the thallus has an unconstricted appearance. Guiry in Irvine and Guiry (1983) suggested removal of this latter series of species to a separate genus, *Chondrothamnion* Kützing (1843). In accordance with Guiry's opinion, *L. lubrica* should also be transferred to genus *Chondrothamnion*. Further study is required and should include *L. articulata* and *L. clavellosa*, which is the type species of genus *Chondrothamnion*.

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鈴木雅大，吉﨑　誠：**マサゴシバリ目の分類学的研究（1）イトタオヤギソウ（フシツナギ科，紅藻）の体構造と生殖器官**

青森県佐井村で採集したイトタオヤギソウについて，体構造，生殖器官の詳細な形態観察を行った．本種の雄性配偶体と果胞子体形成過程の観察は，初めての報告である．体は多軸型構造で中空，1層の皮層と2，3層の内層が内腔を囲む．皮層細胞は周りに小細胞を生じる．内層細胞は皮層細胞を縦方向に裏打ちし，球形の腺細胞を単独に生じる．プロカルプは，3細胞からなる造果枝と，2細胞からなる1本の助細胞枝で構成される．受精後，造果枝を構成する細胞は融合し，造果枝融合細胞は助細胞と直接接触する．助細胞はゴニモブラストを生じ，ほとんどのゴニモブラストが果胞子となる．果胞子体は果皮に覆われる．成熟した嚢果は壺形で，果孔を持つ．精子嚢は，皮層細胞の上に形成された母細胞から切り出される．四分胞子嚢は，皮層細胞に頂生し，三角錐状に分裂し，体表面に作られたくぼみの中に集まって形成される．

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